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HABITAT USE BY COLONIES OF *PHILOPONELLA REPUBLICANA* (ARANEAE, ULOBORIDAE)

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ABSTRACT

Philoponella republicana (Araneae, Uloboridae) is a communal orb-weaving spider. Colonies of this spider were found more frequently in interface forest than in high forest or mountain savannah forest. This does not appear to be due to differences in insect abundance among forest types, but is correlated with greater complexity of the understory in the interface forest. This may be due to the need for supports for colony attachment lines. Within the interface forest, the location of colonies is correlated with local insect abundance. When flying insects are excluded from colonies, individual spiders can respond by increasing the distance between orbs in the colony, and colonies can respond by abandoning the site and moving to a new location.

INTRODUCTION

Philoponella republicana (Simon) is a communal orb-weaving uloborid spider, found in Panama, Trinidad, and northern South America (Opell 1979). It occurs in the rainforest understory, frequently in small tree-fall gaps and other openings in the forest. It is a seasonal species, with as many as three discrete generations per year in Panama (Lubin 1980).

The colonies consist of attachment lines, individual prey capture orbs, and a central retreat area (Figure 1). The retreat is an irregular tangle of non-sticky threads; individuals leave their orbs and move to the retreat in the evenings and when disturbed. Females with egg-cases and adult males may also spend much of their time in the retreat (see also illustration in Simon 1891). Prey capture generally takes place in the orbs. The orbs are placed above and around the retreat, sometimes several layers deep (rarely directly below the retreat); orbs are occupied by one individual at a time. The body of the colony is suspended a short distance above the ground by the attachment lines. These are large conspicuous bundles of non-sticky threads running from the colony to objects in the environment used as supports (e.g., shrubs, herbs).

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The communal societies of *P. republicana* are simple compared with those of cooperative spider species such as *Agelena consociata* (Agelenidae; Kraft 1970), *Anelosimus eximius* (Theridiidae; Brach 1975, Christenson 1984, Vollrath 1982), or *Stegodyphus sarasinorum* (Eresidae, Jambunathan 1905). There is no maternal care of the young other than guarding the egg-case, and no cooperation in orb construction. Nor do females cooperate in prey capture: although several females may be attracted to a large struggling insect and help to wrap it, a short aggressive interaction ensues and one female claims the prey packet. There may, however, be more integration of colony members than this description implies, since colony mates share the support lines and the retreat, and there is some evidence (presented below) that the colony may respond as a group to unfavorable conditions.

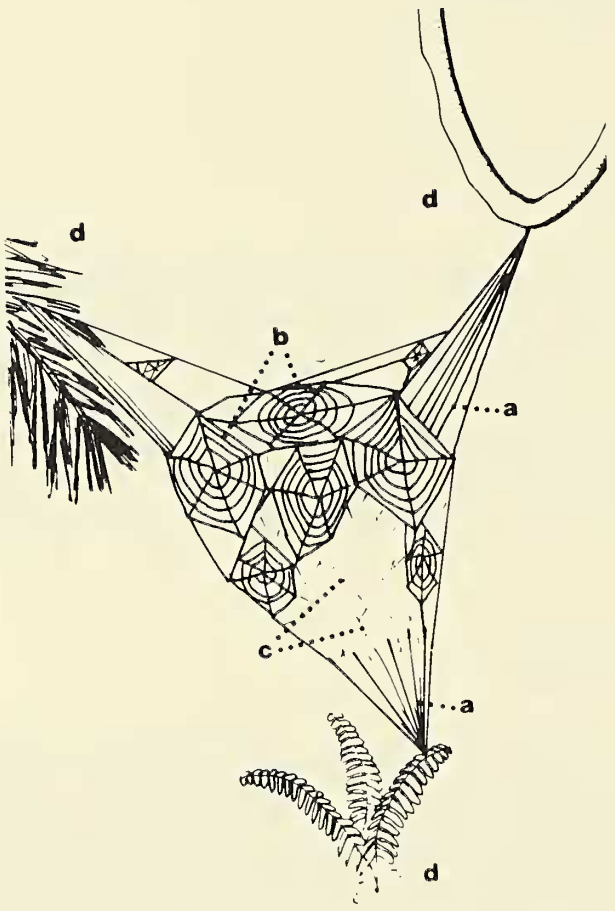

Fig. 1.—Sketch of a *Philoponella republicana* colony; a = support lines; b = individual prey capture orbs; c = central retreat area; d = objects used as supports (herbs, lianas, palms).

Study of the facultatively communal species *Philoponella oweni* in Arizona, U.S.A. (Smith 1982, 1983) showed that this species forms communal groups in response to several environmental factors. *Philoponella oweni* builds its long-lasting webs in protected sites, such as hollow trees or clefts among rocks. These sites may be scarce in some habitats, and the same sites are often used year after year by succeeding generations. Females are solitary if such sites are abundant, or if food is scarce. Communal groups form in areas where suitable sites for web construction are in short supply and insects are locally abundant, allowing several females to share a protected site and still obtain enough prey.

Lubin (1980) reports that new colonies of *P. republicana* are often founded by groups of immatures dispersing *en masse*. It is possible that *P. republicana,* with its larger and more complex groups, has evolved from an ancestor in which groups of immatures responded to patchily distributed resources in a way similar

to that of *P. oweni*. For instance, if food were abundant groups of siblings might remain together, whereas if food were scarce they would disperse. Later they might evolve the habit of remaining in groups even when local food supplies were low, moving as a group to a better location.

Here I examine the location of *P. republicana* colonies with respect to those environmental factors already known to be important to *P. oweni*—insect abundance and substrates for web attachment—and with respect to forest type. I also present natural history information on colony size and development.

METHODS

Forest type.—I carried out observations of *P. republicana* in the Voltzberg-Raleighvallen reserve, Saramacca Province, Suriname (04° 32' N, 56° 32' W) during February-April 1980 and February 1982. The Voltzberg reserve is located in primary lowland rainforest. The vegetation of Suriname is relatively well known and several forest types have been described from the Voltzberg region. The names used here for forest types, and the brief descriptions below follow Schultz (1960).

High forest is characterized by having two or three stories, the lower stories appearing very open. The main canopy is ca. 30 m tall, with emergent trees reaching about 40 m. Palms, particularly "*boegroe makka*" (*Astrocaryon sciophilum*), are abundant in the understory and form a fairly continuous layer at ca. 8 m. The understory is sparse.

Mountain savannah forest is a semi-deciduous forest which occurs on shallow stony soils, as on the edges of granite plates and bergs. It resembles true savannah somewhat in appearance (hence the name) but differs floristically. Trees are thin-stemmed and there is little stratification. There may be a dense herb layer.

I also included a third type: interface forest. Interface forest occurs where two or more forest types meet. This forest is characterized by a very dense understory of palms, lianas, shrubs, woody plants and herbs.

The forest in the Voltzberg reserve was essentially undisturbed except for trails, which passed through tracts of each of the three forest types mentioned here. I located colonies by searching along trails; because the trails did not pass through equal distances of each forest type, the amount of each forest type sampled was not equal. The understory in mountain savannah forest was much less dense than in either high or interface forest; although colonies a few meters off the trails in the latter two forest types might not be visible, one could easily see objects which were reasonable distances from the trail in mountain savannah forest.

Insect Abundance.—I measured insect abundance using sticky traps; my traps were fresh-cut leaves of *Heliconia* sp. (Because all equipment and food for two weeks at a time had to be backpacked into the study area, it was necessary to rely on natural materials as much as possible. I selected *Heliconia* leaves because they were large, abundant, and relatively uniform in size, and provided a smooth tough surface to spread the trap substance on.) I traced a 15 X 30 or 10 X 20 cm rectangle on the underside of the leaf, and coated an area larger than the rectangle with Stick'em Special. Insects which crawled onto the leaves would

presumably be caught before they reached the rectangle; insects captured inside the rectangle were assumed to be flying insects. By coating the underside of the leaf I ensured that the trapping surface would not be obscured if the leaf began to wilt. The leaf traps were suspended from trees and saplings.

I measured insect abundance at colony sites and at non-colony sites using a paired sampling scheme. I placed a *Heliconia* leaf trap next to each of seven colonies at the same height as the colony's prey capture surface, and a second trap at an arbitrarily chosen site 5 m due north, at the same height. Two trap sizes were used in different trials—10 X 20 and 15 X 30 cm. The traps in any paired comparison were the same size. In most cases the traps were examined after 24 hrs, but in some cases pairs were examined after 48 or 72 hours. I analyzed these data with the Wilcoxon signed rank test for paired comparisons (Seigel 1956) to allow for the variation in size and time among pairs. When traps were examined I recorded the number of insects captured, their size (length to the nearest mm; insects less than 1 mm were placed in one of two size classes: those less than 0.25 mm, and those greater than 0.25 mm and less than 0.5 mm), and taxonomic order.

I also compared insect abundance in the three forest types. I placed five *Heliconia* leaf traps with a 10 X 20 cm capture area in each forest type. Points for trap placement were randomly selected by laying a 50 m forester's tape along a trail passing through the appropriate forest type, and selecting two numbers from a random number table. The first number dictated how many meters I moved along the meter tape, the second how many meters I moved into the forest perpendicular to the tape, alternating left and right of the tape. I collected data on the number of insects captured as above, every 24 hours for five days.

Not all insects captured in sticky traps are potential prey for *P. republicana*. *Philoponella republicana* typically takes insects 5 mm or less in total body length, and usually does not take Orthoptera or Hemiptera (personal observation). I called the subset of insects captured that were 5 mm or less in length, exclusive of Orthoptera and Hemiptera the "small insects." The potential prey truly available to *P. republicana* probably consists of some of the "small insects" and also some insects not captured by the sticky traps at all. During data analysis I used four measures of insect abundance—total number of insects captured per trap per day, total number of "small insects" captured per trap per day, sum of the lengths of all insects captured per trap per day, and the sum of lengths of "small insects" per trap per day. Although watching actual prey capture is the best way to assess what a particular spider species is taking (Castillo L. and Eberhard 1983), this method cannot be used to compare insect abundances in habitats where spiders occur and where they do not. The sticky trap data can be useful to compare abundance of certain classes of insects among different locations, but cannot be used to calculate total insect prey available.

Forest understory.—I measured the structure of the forest understory at the sites of five *P. republicana* colonies and in each of the three forest types to find the relative numbers of potential supports for colony attachment lines. I randomly selected 10 points in each forest type using a meter type and random number table as described above. At 1 m north, south, east and west of each randomly chosen point I suspended a 160 cm plumb line and recorded the number of plant stems and leaves that intersected the line. At colony sites I took

measures 1 m north, south, east, and west of the center of the colonies. The total number of plant parts intersecting the four plumb lines for each point were summed for each point, since the four were not independent measurements. If a plumb line fell on a point occupied by a tree or boulder, that point was discarded.

Food Deprivation.—Orb-weaving spiders can respond in a number of ways to decreasing food supplies, for example by spinning larger orbs or by relocating the web. In communal groups spiders can also change the distance between orbs (a change in the diameter of the orb can also cause a change in orb spacing). I measured the response of colony members to food deprivation in terms of the distance between an orb and its nearest neighbor. I first gathered six days of baseline data on the nearest neighbor distances (NND) in three unmanipulated colonies (No. 1, 4, and 5). Each day I measured the distance (to the nearest cm, hub to hub) to the nearest neighboring orb for 10 to 22 orbs in each colony. If the orbs were readily accessible I measured the distance with a ruler. If direct measurement would have disturbed the spiders or the webbing I estimated the distance. To test the accuracy of my estimates I first estimated the NND's for a set of readily accessible orbs, and then measured the distance. My estimates were not significantly different from the direct measurements.

Next I built a large tent around colony 1. The tent consisted of a framework of saplings and rope covered with cheese cloth. The tent was left in place for five days, during which time it excluded most flying insects from the colony. After five days I measured NND for orbs in the experimental and two control colonies.

I repeated the experiment using colonies 3, 4, and 5. I gathered baseline data for one day and then built a cage around colony 3. After three days of insect exclusion I measured NND in the experimental and control colonies.

To test for the effect on NND of general disturbance during tent building I gathered baseline data for one day on colony 8 and then built a tent framework around it, consisting of poles and ropes without the cheese cloth. I recorded NND in this colony for three more days.

Colony growth and size.—I censused seven *P. republicana* colonies (No. 1 and 3-8) from 11 February to 10 April 1980. I classed the spiders in the colonies as adult males, adult females (7 mm or more in total body length) or one of four size classes of immatures: less than 1 mm, 1-2 mm, 3-4 mm, and 5-6 mm. When counting numerous tiny hatchlings much less than 1 mm in length I took three counts and used the average.

I measured the size of four colonies: height and horizontal diameter of the main body of the colony (retreat plus orbs) and number and length of attachment lines, all to the nearest 10 cm. I also noted the objects used as supports for the attachment lines.

RESULTS

Forest type.—In 1980 I located seven (or five—see the section on Food Deprivation below) large colonies of *P. republicana.* These colonies were in interface forest (five colonies) or in gaps in forest created by boulder fields (two colonies). The trails passed through large tracts of high forest and mountain

Table 1.—Mean number of insects of all types captured per sticky trap per day in three Suriname forest types. Trap sites are of three types: random sites were randomly selected points in each forest type; arbitrary sites were 5 m due north of *Philoponella republicana* colonies in interface forest; colony sites were next to colonies of *P. republicana*. Data from all trap sites were compared using the Mann Whitney U-test. Means with the same group letter do not differ significantly at the 0.05 level.

Forest type:	Trap site	Mean	SD	N	Group
High	random	3.6	2.5	25	A
Mt. Savannah	random	5.2	3.0	25	B
Interface	random	5.8	3.8	25	B
	arbitrary	5.3	3.5	28	B
	colony	7.9	4.2	28	C

savannah forest and only a small belt of interface forest. Because most of the colonies were found in interface forest, even though less of this forest type was sampled, this implies that *P. republicana* occurs more frequently in interface than in high or mountain savannah forest.

Insect abundance.—Insects were more abundant at colony sites than at arbitrarily selected sites 5 m north of colonies for all four measures of insect abundance: total number of insects ($p << 0.01$), total number of "small insects" ($p << 0.01$), sum of lengths of all insects ($p < 0.01$), and sum of lengths of "small insects" ($p << 0.02$) captured per trap per day (Wilcoxon signed rank test for paired samples, Seigel 1956).

A comparison of insect abundance in the three forest types is given in Table 1; these data were analyzed using three-way Analysis of Variance and Duncan's multiple range test (Barr et al. 1976). There is no difference in the mean number of insects captured per trap day in interface and mountain savannah forest, and significantly fewer captured per trap day in high forest than in the other forest types. It is also possible to compare insect abundance at these randomly selected points in the three forest types with insect abundance at colony sites and the arbitrarily chosen points 5 m north of colonies (Table 1). Data from 28 pairs of traps of the same size and duration of exposure as the forest samples (10 X 20 cm, 24 hrs) showed that there were significantly more insects captured per trap/day at colony sites (7.9 ± 4.2) than in any other site (Mann Whitney U-test, $p < 0.04$ or better). There was a mean of 5.3 ± 3.1 insects per trap/day at sites 5 m north of colonies, which is not significantly different from the values for randomly selected points in interface or mountain savannah forest ($p > 0.75$, Mann Whitney, U-test).

Understory structure.—Table 2 shows the complexity of the understory in three forest types and at sites occupied by colonies. There is no significant difference in the mean number of plant parts intersecting plumb lines in interface forest and at colony sites, and there is also no significant difference between high and mountain savannah forest in this respect. There are significantly more plant parts—potential web supports—in colony sites and in interface forest than in high and mountain savannah forest.

Food deprivation.—In replicates 1 and 2, in which functional insect exclusion tents were used, the NND increased when insects were excluded. In replicate 1

Table 2.—Structure of the forest understory: mean number of plant parts intersecting four 160 cm plumb lines in three forest types and at sites of *Philoponella republicana* colonies. Means with the same group letter do not differ significantly at the 0.05 level. Interface differs from High and Mountain Savannah forest at $p<0.002$; Colony sites differ from High and Mountain Savannah forest at $p<0.05$ (Mann Whitney U-tests).

Forest type:	Mean	SD	N	Group
High	2.3	1.6	10	B
Mt. Savannah	1.6	1.8	10	B
Interface	9.9	2.8	9	A
Colony	6.8	2.9	4	A

the NND in the experimental colony increased from 8.2 ± 1.5 cm (n = 19 orbs) on the day before insect exclusion to 11.1 ± 3.7 cm after exclusion (n = 17; $p < 0.02$, two-tailed Mann Whitney U-test; Seigel 1956). There was no significant change in the NND in the control groups. In control colony 4 the NND was 6.8 ± 1.7 cm (n = 20) before the experiment and 6.8 ± 1.5 after (n = 16; $p > 0.10$); in control colony 5 the NND was 6.1 ± 0.8 cm before (n = 20) and 6.4 ± 1.7 cm after (n = 20; $p > 0.10$).

In replicate 2 the NND in the experimental colony increased from 7.6 ± 2.1 cm (n = 16) on the day before insect exclusion to 11.2 ± 3.8 cm after (n = 18; $p < 0.002$, two-tailed Mann Whitney U-test). In control colony 4 the NND was 7.0 ± 1.7 cm before (n = 20), and 7.1 ± 1.0 after (n = 20; $p > 0.10$); control colony 5 the NND did increase significantly after the course of the experiment ($p < 0.05$) but the magnitude of the change was small (6.7 ± 1.6 cm before, n = 20, to 7.6 ± 0.9 cm, n = 20 after).

In colony 8 the NND did not increase after the sham tent was built. Before the tent was built NND was 12.1 ± 2.1 cm (n = 10 orbs). On the first day after the sham cage was built NND decreased significantly to 9.0 ± 1.5 cm (n = 7; $p > 0.02$). On the next two days NND increased back to values not significantly different from the original values: 11.8 ± 1.7 (n = 7) and 11.0 ± 2.2 (n = 5; $p > 0.10$).

In addition, in replicates 1 and 2 the experimental colony abandoned its old site after the insect excluding tent was removed; apparently the colony moved as a group to a new location. Within a few days after removal of the tent the old site was abandoned and two new colonies, 6 and 7, appeared two to three meters away from the sites of the old colonies 1 and 3. The experimental colony 1 contained three marked individuals, one of whom was later seen in colony 6. In addition a female was seen walking on the ground from near the old site of colony 1 towards colony 6. This circumstantial evidence indicates that each colony moved as a group.

Colony Growth and Size.—Figure 2 presents the development of Suriname colonies over the period from 11 February to 10 April 1980. Hatchlings, i.e., spiderlings in their first post-emergence instar, are easily identified by their non-sticky "sheet" orbs (Eberhard 1971, Szlep 1961). All the hatchlings were found in the attachment lines of the colony, not in the body of the colony. Females with egg-cases often leave the colonies (Lubin 1980) perhaps in an attempt to avoid egg-case parasites. The hatchlings in the attachment lines may be the young

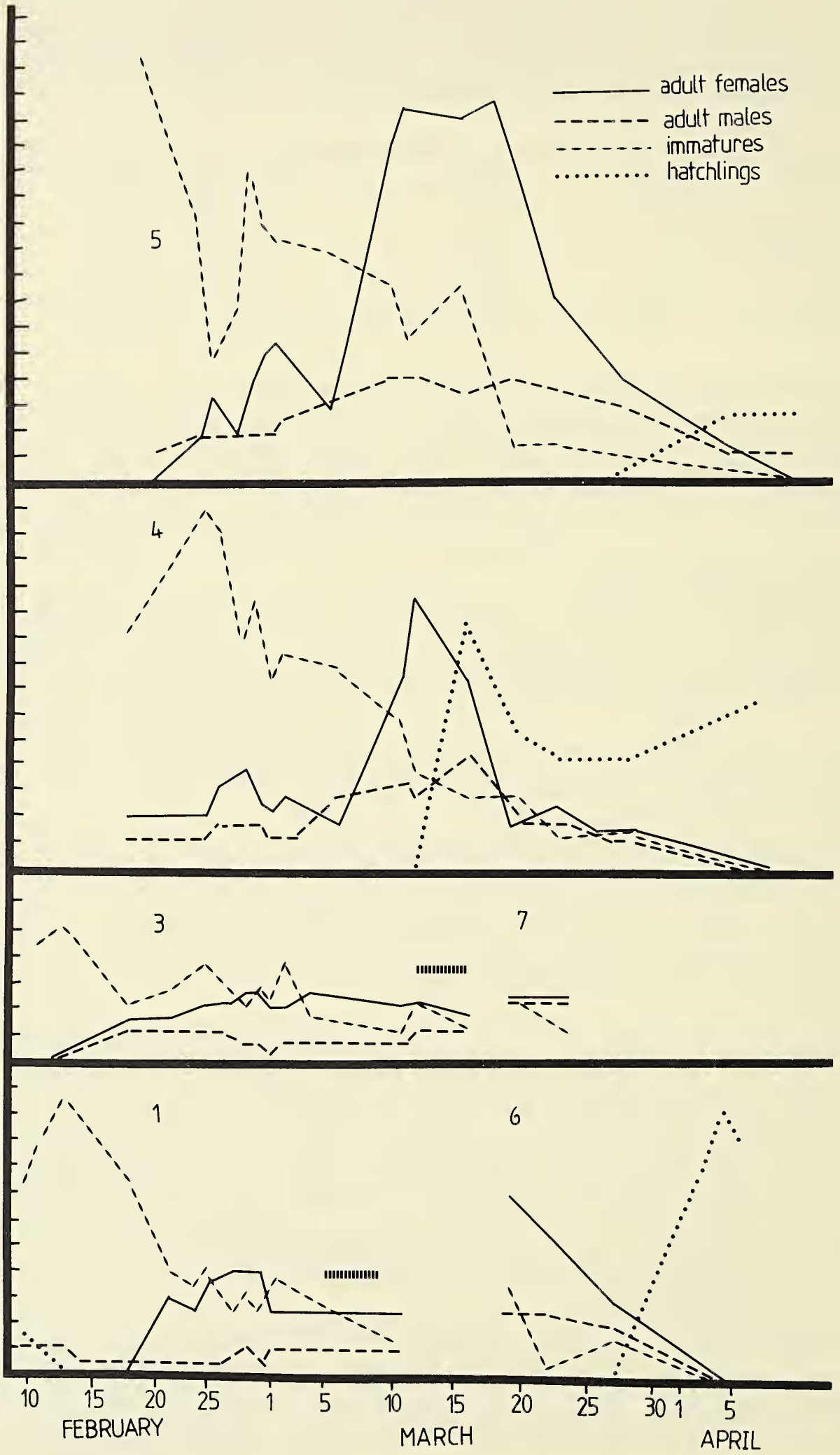

Fig. 2.—Census data from six colonies of *Philoponella republicana* (colonies no. 1, 3, 4, 5, 6, and 7). Horizontal axis, time in days; vertical axis, number of individuals in units of 10; striped horizontal bars, duration of insect exclusion experiments.

of females who left the colony along the attachment lines. The seven colonies were roughly synchronous in development, and most of the adults of a colony die or disappear before the young produced by their generation mature. Thus there is no overlap of adults between generations in these populations.

The four colonies measured to the nearest 10 cm were 85 ± 5 cm tall and 60 ± 0 cm in diameter. The retreats were 0 to 30 cm above the ground. There were an average of 8 ± 2.2 attachment lines per colony, each an average of 78.6 ± 41 cm long (range 40 to 200 cm). The attachment lines were fastened to lianas, leaves of hardwood trees, and most commonly, palms.

DISCUSSION

Colonies of *P. republicana* in Suriname were found more frequently in interface forest than high or mountain savannah forest. This does not appear to be a result of differences in insect abundance among the three forest types, since insects were no more abundant in interface than in mountain savannah or high forest. The size of *P. republicana* colonies, their height above the ground, and the length of their attachment lines means that they are using objects for support from ground level to 1.5 to 2.0 m above the ground. The understory in interface forest is denser than in high or mountain savannah forest and thus provides more potential supports for colony attachment lines.

Within interface forest the location of *P. republicana* colonies does appear to be influenced by insect abundance, inasmuch as colonies were found at sites where insects were locally abundant. (Considering insects caught in sticky traps as a measure of insect abundance.)

Individuals within colonies also respond to changes in insect abundance. If food supplies are reduced by building a cage around the colony, the individual spiders spin their orbs farther apart. When the cage is removed and the colony is given the opportunity to move the group abandons the old, "poor" site and relocates in a new site. Thus this species responds to environmental conditions at three levels: at the level of the forest type occupied, at the level of colony location within the chosen forest type, and at the level of individual spacing within colonies.

The responses of *P. oweni* and *P. republicana* to food supply and web building sites can be compared. *Philoponella oweni,* the facultatively communal species found in the southwestern United States, builds its webs in protected sites which may be in short supply in some habitats. Because the locations of these protected web sites do not change much from year to year, the location of *P. oweni* webs are also rather stable from year to year. Some immatures of *P. oweni* overwinter at their mother's web site and emerge the following spring to begin a new colony. Some sites were occupied by *P. oweni* colonies for at least six consecutive years. The number of adults which ultimately remain at a site appears to be largely governed by insect abundance at the site (Smith 1983). These results agree with those of Uetz et al. (1982), who found that the number of individuals in communal groups of *Metepeira spinipes* (Araneidae) and interindividual spacing within the colonies, varied in response to the abundance of prey.

Compared to *P. oweni,* colonies of *P. republicana* are more mobile. In habitat used by *P. republicana* (interface and second growth forest) suitable attachments for web building appear to be relatively abundant, and the results of the insect exclusion study indicate that a colony may move as a group in response to changes in food supply. Thus, whereas *P. oweni* remains at a web site and adjusts group size to food supply, *P. republicana* maintains its communal group and moves the colony in response to food shortages. This can only be done in habitats where potential web attachment sites are plentiful. *Philoponella republicana* could be derived from a species in which immatures dispersed in groups and responded to changes in food supply by moving the entire group to a better site rather than by breaking up the group into individuals.

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